
WOOD AND BARK ANATOMY *Sherwin Carlquist*¹ OF *TICODENDRON*: COMMENTS ON RELATIONSHIPS

ABSTRACT

The single known species of *Ticodendron* has notably primitive wood (scalariform perforation plates with numerous bars; primary wall remnants in perforations; scalariform lateral wall pitting in vessels; imperforate tracheary elements all tracheids; axial parenchyma diffuse; rays Heterogeneous Type I). Although wood of Betulaceae and Corylaceae (Betulaceae subfamily Coryleae of most authors) is more specialized, primarily in tracheary element morphology and ray histology, wood features in these families are consonant with relationship to *Ticodendron*. Presence of crystals in rays is alike in *Ticodendron*, Corylaceae, and Fagaceae. Bark anatomy features are shared by the fagalean families: fusiform-shaped nests of sclereids containing large rhomboidal crystals; druses in cortex, phloem parenchyma, and ray parenchyma; and subdivision of ray cells that contain druses. Placement of *Ticodendron* in Fagales as a separate family, more primitive than others in the order, is indicated by the data reviewed.

Wood anatomy is of interest in phylogenetic studies because it contains characters that suggest relationship, as well as characters that are sensitive indicators of ecology and of degree of primitiveness and specialization. Bark anatomy, if not as rich in characters, does contain certain character assemblages indicative of relationship. The discovery of the distinctive tree *Ticodendron* (Gómez-Laurito & Gómez P., 1989) provides an opportunity for the use of wood and bark anatomy in order to determine the relationships of this interesting genus.

The samples of *Ticodendron*, provided me by Peter H. Raven and Barry Hammel of the Missouri Botanical Garden, proved excellent material for analysis of anatomical features. Liquid-preserved stems 37 mm diam. with thin bark were collected by Gordon McPherson (11659, MO) at Fortuna Dam, Chiriquí, Panama. A dried section of a large log (about 40 cm diam.) with bark 6 mm thick was collected by William A. Haber (7071, MO) at Peñas Blancas, east of Monte Verde, Costa Rica. Viewed together, these samples permit study of a broad range of histologic and ontogenetic aspects of wood and bark.

Comparison of wood and bark anatomy of *Ticodendron* with that of other dicotyledons is the main focus of this study because of the distinctive features and apparent isolation of the genus. For this purpose, the wood slide collection at the Rancho Santa Ana Botanic Garden proved unusually valuable because of its size and because some of

the wood sections in this collection have bark attached to them. The data below show that bark seems unusually decisive in determination of relationships of *Ticodendron*.

Regardless of systematic position, *Ticodendron* possesses a constellation of characters that must be judged unusually primitive for a vessel-bearing dicotyledon. These wood features offer an unusual dimension, because one might not have guessed that the moderately specialized floral features of the genus are coupled with such primitive wood. Wood of this type is related to occupancy of mesic sites (Carlquist, 1975), and thus wood of *Ticodendron* is of interest with relationship to ecology as well.

MATERIALS AND METHODS

A wood segment from near the cambium and a bark portion were taken from the large dried trunk section *Haber 7071*. These were boiled in water and stored in 50% aqueous ethyl alcohol. Similar segments of *McPherson 11659*, a liquid-preserved collection, were transferred to 50% aqueous ethyl alcohol. Wood and bark of both collections were sectioned on a sliding microtome without softening agents. Some sections of *McPherson 11659* were dried between glass slides and examined with a scanning electron microscope. Sections for light microscope study were stained in safranin and lightly counterstained with fast green to improve con-

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trast of pit details. Macerations were prepared with Jeffrey's fluid and stained with safranin.

Mean number of vessels per group is calculated on the basis that a solitary vessel is rated 1, a pair of vessels in contact is rated 2, and so forth, and 25 such figures are averaged. Vessel diameter is based on lumen diameter at widest point. Means for quantitative features are based on 25 measurements except for vessel wall thickness, tracheid diameter, and tracheid wall thickness; for these features, a few typical conditions were selected and averaged.

ANATOMICAL DESCRIPTIONS

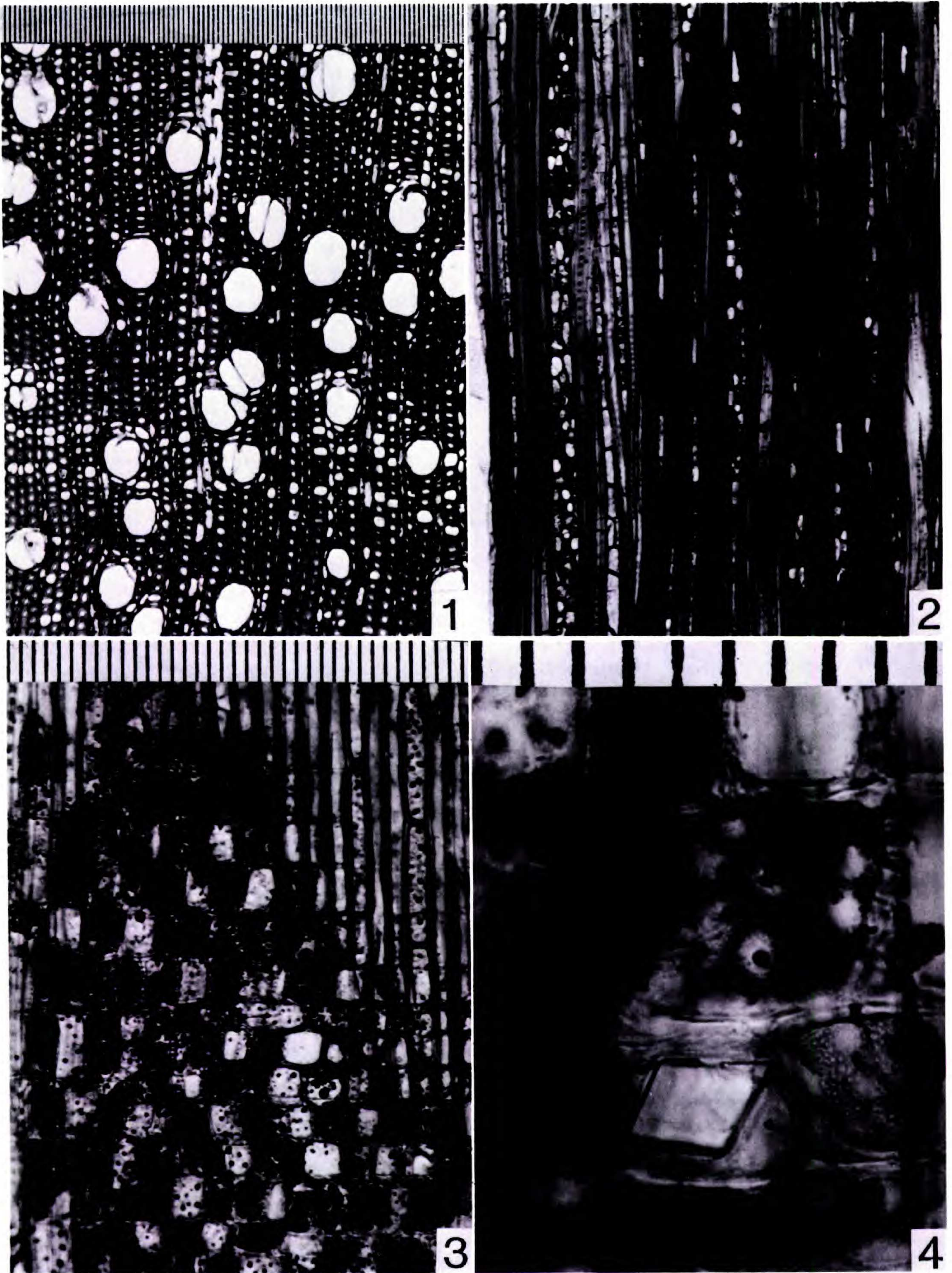
WOOD

A full description is given here for the sample *McPherson 11659*. Data are then given for *Haber 7071*, but the latter description is limited to features in which this wood sample differs from *McPherson 11659*.

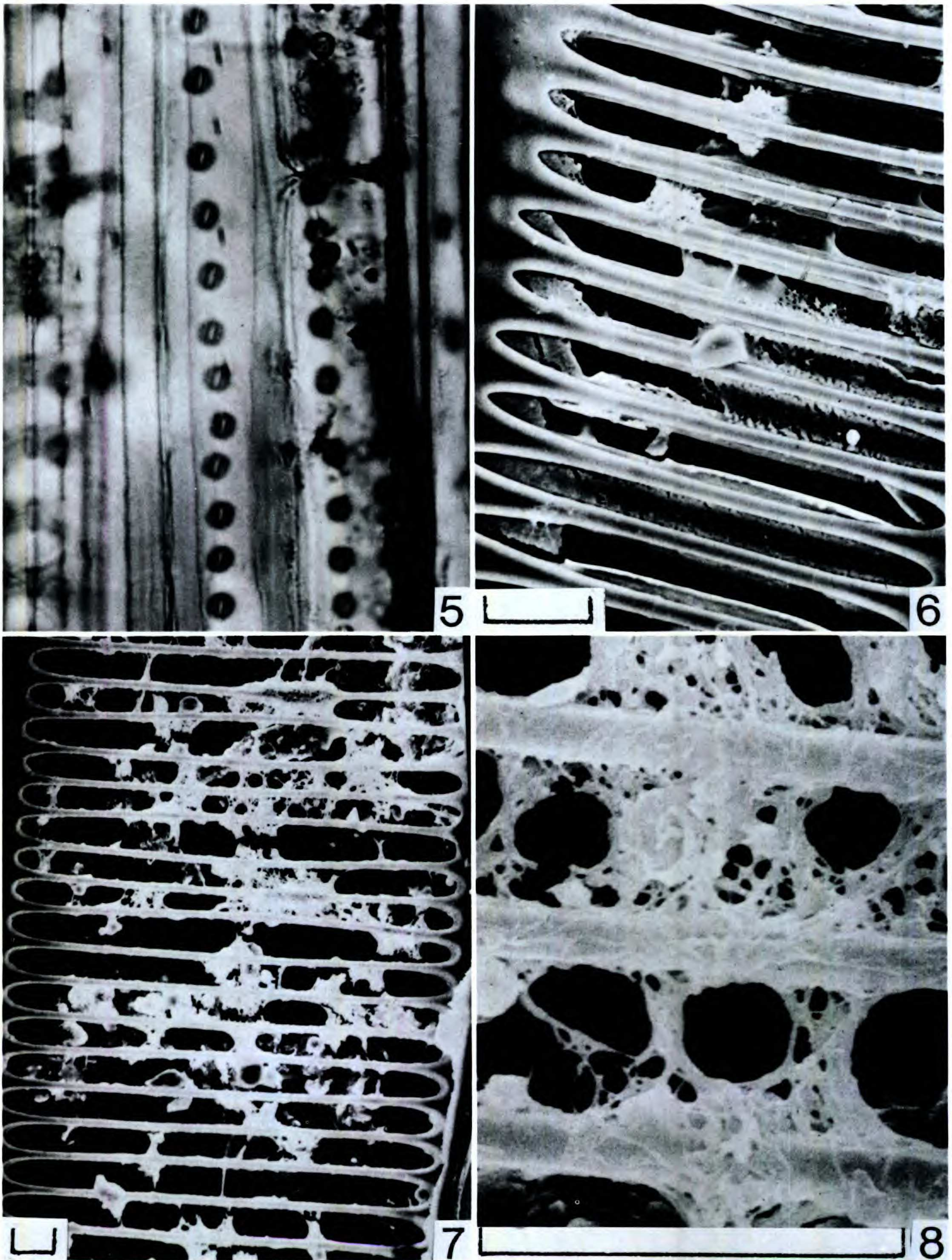
Ticodendron incognitum Gómez-Laurito & Gómez P., *McPherson 11659* (Figs. 1–15). Growth rings essentially absent; a small fluctuation in vessel diameter observable (narrower vessels one-third of the way from bottom of photo, Fig. 1). Vessels solitary, rarely in pairs (Fig. 1). Mean number of vessels per group, 1.04. Mean vessel diameter, 73 μm . Mean number of vessels per mm^2 , 23. Mean vessel element length, 1,725 μm . Mean vessel wall thickness, 2.6 μm . Perforation plates scalariform (Figs. 6, 7), all bars bordered, borders wider at ends of perforations (Fig. 7). Mean number of bars per perforation, 62. Perforation plates frequently with meshlike pattern in this sample (Figs. 9–11). Primary wall remnants in perforation plate extensive (Figs. 6, 10, 11) to moderate (Figs. 7, 8), mostly the latter, but with some vestiges of pit membranes present in all perforation plates. Moderate remnants take the form of webs and strands (Figs. 7, 8), or have a clotted appearance (Fig. 11), the latter possibly the result of inhibition of enzymatic pit membrane dissolution by deposition of some secondary plant products. Primary wall remnants in perforations may show various sizes of micropores (Fig. 8). Lateral wall pitting of vessels scalariform, less commonly transitional or opposite, on vessel-axial parenchyma (Fig. 13) and vessel-ray contacts. Vessel-tracheid contacts bear circular to oval pits alternate in arrangement but often rather sparse (Fig. 12). Vessels rounded in transectional outline (Fig. 1). Imperforate tracheary elements are all tracheids with fully bordered pits, pit cavities about 4 μm diam. (Fig. 5). Mean tracheid length, 2,473 μm . Mean tracheid diameter

at widest point, 29 μm . Mean tracheid wall thickness, 6 μm . Pits are somewhat more abundant on tangential walls of tracheids than on radial walls, as determined from study of transections. Axial parenchyma moderately abundant and chiefly diffuse, with tendencies toward diffuse-in-aggregates and abaxial occurrence (Fig. 1). Axial parenchyma strands often about 14 cells long, the mean length of each component cell about 150 μm . Rays both multiseriate and uniseriate, about equal in frequency (Fig. 2). Mean height of multiseriate rays, 1,193 μm . Mean height of uniseriate rays, 594 μm . Mean width of multiseriate rays at widest point, 3.2 cells. Multiseriate rays mostly with a uniseriate wing at one or both tips. Uniseriate rays and uniseriate wings of multiseriate rays composed of upright cells. Upright cells also present adjacent to wings of multiseriate rays and occasional as sheath cells in multiseriate rays (Fig. 2). Procumbent cells present in multiseriate portions of multiseriate rays, not much longer horizontally than vertically (Fig. 3). Rhomboidal crystals present singly in a scattering of ray cells (Fig. 4), the crystals more abundant in the transition from one year's wood to the next. Starch grains spherical (Fig. 14) to slightly angular (Fig. 15), abundant in axial parenchyma (Figs. 3, 14) and in ray cells (Figs. 4, 15). Dark-staining "resinlike" compounds present in many (but not all) ray cells (Figs. 2–4). Unidentified smaller spheroidal bodies present in ray cells (Fig. 15).

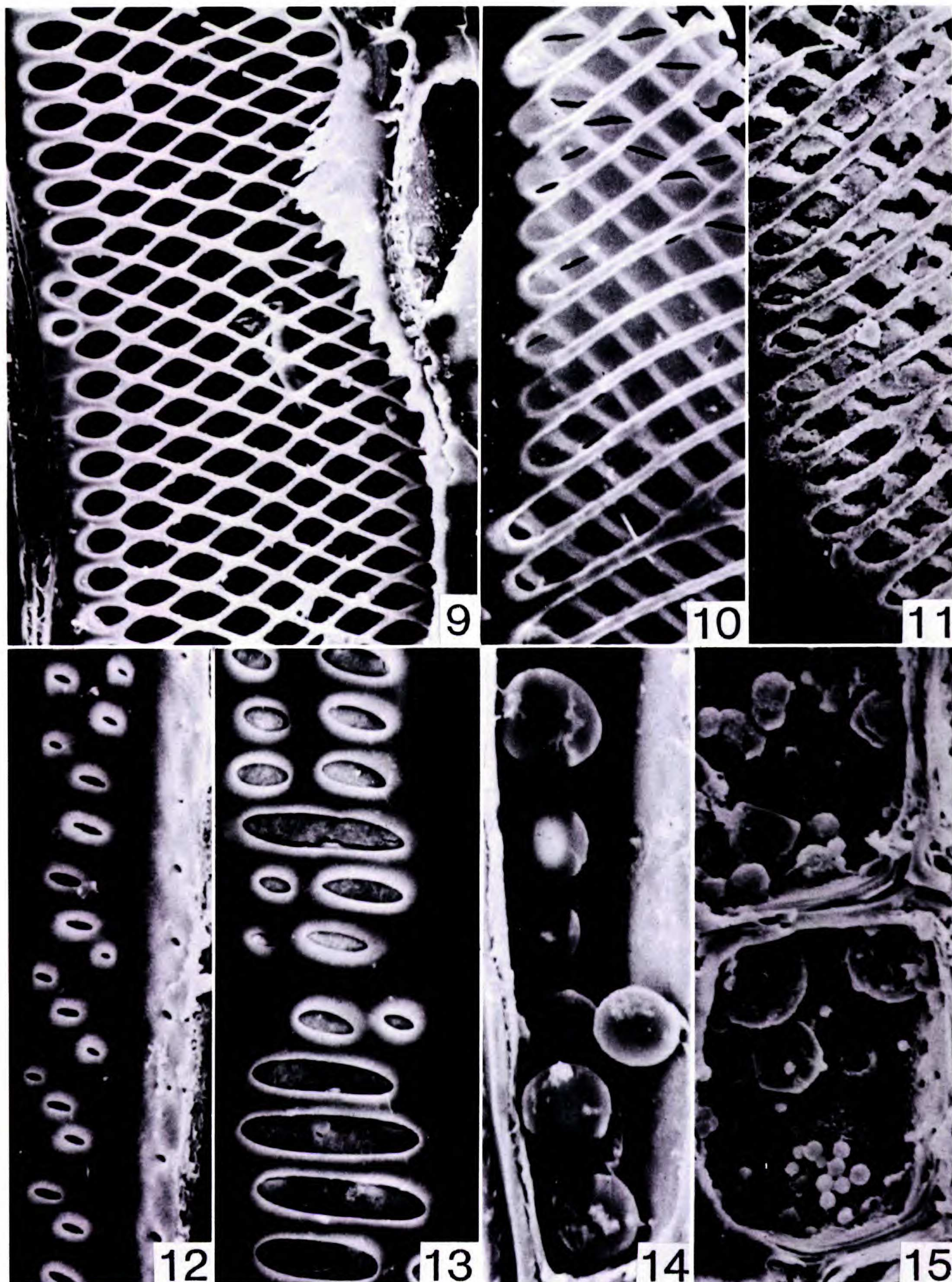
Ticodendron incognitum, Haber 7071. Mean number of vessels per group, 1.13. Mean vessel diameter, 116 μm . Mean number of vessels per mm^2 , 22. Mean vessel element length, 1,782 μm . Mean vessel wall thickness, 2.6 μm . Perforation plates scalariform (no meshworklike patterns observed). Mean number of bars per perforation plate, 32. Primary wall remnants in perforations (as observed by light microscopy) minimal. Mean tracheid length, 2,537 μm . Mean tracheid diameter at widest point, 31 μm . Mean tracheid wall thickness, 7.2 μm . Axial parenchyma diffuse (sparser than in *McPherson 11659*), with a slight tendency toward diffuse-in-aggregates and abaxial arrangements. Mean height of multiseriate rays, 2,312 μm . Mean height of uniseriate rays, 525 μm . Mean width of multiseriate rays at widest point, 6.0 cells. Uniseriate rays and uniseriate wings of multiseriate rays composed of upright cells. Multiseriate portions of multiseriate rays composed of procumbent cells, with only a few upright sheathing cells present. Procumbent cells radially elongate (radial dimension 1.5–8 \times the vertical dimension). Crystals



FIGURES 1-4. Wood sections of *Ticodendron incognitum*, McPherson 11659.—1. Transection; vessels are solitary (pair of vessels in contact, center).—2. Tangential section; rays conform to Kribs's Heterogeneous Type I.—3. Radial section; ray in sectional view, showing starch (hila = dark dots) and dark-staining compounds; cell shapes vary between square and upright.—4. Radial section, showing rhomboidal crystal, starch grains, and dark-staining compounds. Figures 1, 2, magnification scale above Figure 1 (divisions = 10 μm). Figure 3, scale above Figure 3 (divisions = 10 μm). Figure 4, scale above Figure 4 (divisions = 10 μm).



FIGURES 5-8. Wood sections of *Ticodendron incognitum*, McPherson 11659. —5. Radial section, showing pits on tracheid in face view (center) and sectional view (left). 6-8. Perforation plates from radial sections, SEM photographs. —6. Perforation plate bearing large intact portions of pit membranes. —7. Perforation plate bearing threadlike and weblike portions of pit membrane. —8. Perforation plate portion, showing micropores among microfibrillar webs of pit membranes in perforations. Figure 5, magnification scale above Figure 4. Figures 6-8, scale indicating magnification (bracket = 10 μm at bottom of respective figures).



FIGURES 9-15. SEM photographs of wood sections of *Ticodendron incognitum*, McPherson 11659. 9-11. Perforation plates from radial sections, showing meshlike patterns.—9. Perforation plate with minimal remnants of pit membranes.—10. Perforation plate portion with nearly intact pit membranes in perforations.—11. Perforation plate portion with irregularly dislodged pit membrane portions.—12. Vessel—tracheid pitting from radial section (vessel side shown).—13. Vessel—axial parenchyma pitting from radial section (vessel side shown).—14. Starch grains in axial parenchyma cell, from radial section.—15. Starch grains and smaller spheroids in ray cells, from radial section. Figure 9, magnification scale at bottom of Figure 7. Figures 10-15, magnification scale at bottom of Figure 6.

occasional in ray cells (more abundant than in *McPherson 11659*).

The ways in which *Haber 7071* differs from *McPherson 11659* are to be attributed most to different sizes and therefore ages of the samples. Although the wood of *McPherson 11659* does not represent a juvenile pattern, its features can be described as more mature than *Haber 7071* with respect to vessel diameter, multiseriate ray height and width, and degree of radial elongation of procumbent ray cells. The meshlike perforation plate pattern, so abundant in *McPherson 11659*, may be a juvenile feature. This pattern is perhaps less an anomaly than one might think. If a vessel in which bars of a perforation plate follow an oblique or diagonal pattern rather than a strictly horizontal one, a meshlike pattern occurs where the perforation plates (which are combinations of secondary walls of two adjacent cells) occur. The two collections differ slightly in crystal abundance, a feature that sometimes is related to age in dicotyledons.

BARK

The collection *McPherson 11659* (Figs. 16–19) is used as the basis for description; features by which *Haber 7071* differs are given in a later paragraph.

Druses are present in cortical cells (Fig. 17, right), phloem ray cells (center strip two cells wide, Fig. 18), and axial phloem parenchyma cells (Fig. 18, upper left and lower right). Only a fraction of the axial phloem parenchyma cells contain druses. Thus, when axial phloem parenchyma cells develop thick lignified walls (Fig. 17), only a few of these sclereids contain druses. Druses occur in “chambered” fashion in ray cells that are subdivided horizontally, each cell with a single druse.

In older parts of the secondary phloem (Fig. 17), sclereids derived from sclerification of axial phloem parenchyma cells occur in patches. Analysis of longisections shows that these sclereids are not fibers, because they are subdivided into strands as are xylem axial parenchyma; they are also wider than fibers typically are.

Nests of sclereids form in the cortex (Fig. 19), as well as in the old secondary phloem. In the phloem, the sclereid nests evidently are derived from axial phloem parenchyma, but develop into cells much larger and more nearly isodiametric in shape than the sclereid strands mentioned in the above paragraph. In three dimensions, the sclereid nests are often fusiform in shape, the long axis paralleling the stem axis. Many of these sclereids contain one large rhomboidal crystal each (Fig. 19).

The surface of *McPherson 11695* (Fig. 16, top) demonstrates a periderm with about 10 layers of highly compressed phellem cells; this periderm is a dark band in this photograph.

Dark-staining compounds are evident in many cells of the secondary phloem (Figs. 16–19). Cells that contain druses usually do not also contain the dark-staining compounds.

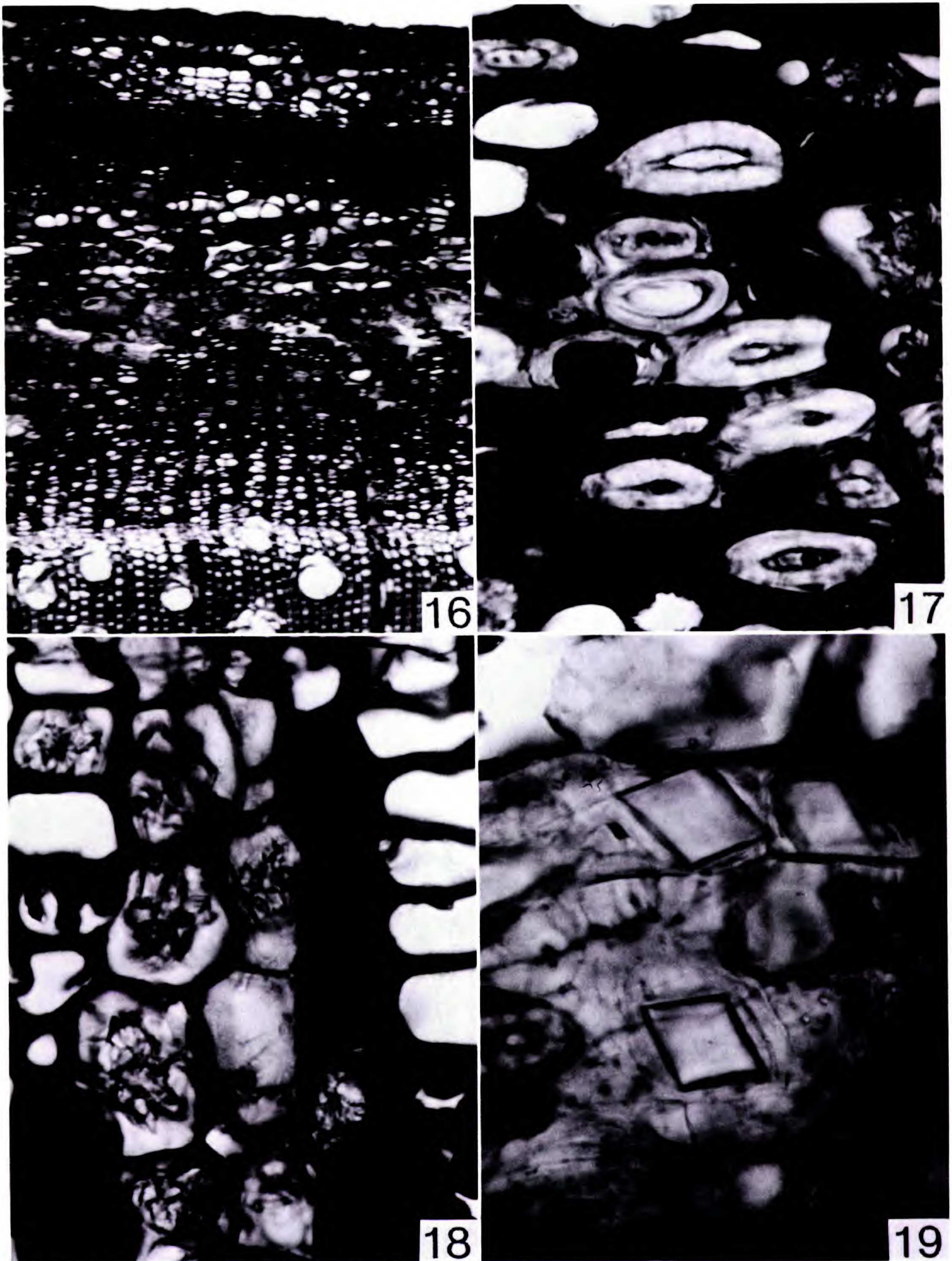
The thick bark of *Haber 7071* reveals several differences. Periderm was not observed in this bark; evidently it had sloughed off and no new periderms originate at levels deep in the bark. *Haber 7071* contains a large number of patches of the sclerified phloem parenchyma strands, but nests of large sclereids, some of which cells contain rhomboidal crystals, are also present. These differences are probably related to age rather than to genetic distinctness.

RELATIONSHIPS OF *TICODENDRON*

Wood of *Ticodendron* is exceptionally rich in primitive features. This suggests unbroken occupancy by this phylad of mesic areas, according to earlier considerations (Carlquist, 1975). Features of *Ticodendron* wood that are regarded as primitive and the authorities for those interpretations in dicotyledons at large are as follows: long vessel elements (Bailey & Tupper, 1918); perforation plates scalariform with numerous bordered bars (Frost, 1930); perforation plates with remnants of pit membranes (Carlquist, 1988: 56–60); tracheids present as the imperforate tracheary element type (Metcalf & Chalk, 1950: xlv, “fibers with distinctly bordered pits”); axial parenchyma diffuse (Kribs, 1937); rays Heterogeneous Type I (Kribs, 1935). Primitive wood features are not by themselves evidence of relationship, for they may be retained in many phylads of dicotyledons independently.

The presence of crystals in rays of *Ticodendron*, a feature that is neither primitive nor specialized, is not evidence of relationships because the number of families that have rhomboidal crystals in rays is quite large (Carlquist, 1988: 225–228). Crystal presence in wood also must be interpreted in a larger context: crystals are more often present in leaves and in primary stems than in wood, suggesting that absence of crystals in wood should be considered significant only if crystals are also absent elsewhere in the plant.

In searching for woods that may resemble that of *Ticodendron*, difference in evolutionary level (especially if moderate) does not rule out relationship provided that there are no features with distinctive systematic distribution that would contra-



FIGURES 16-19. *Ticodendron incognitum*, McPherson 11659, views of bark transections.—16. Transection; small portion of secondary xylem, below, periderm at top (dark); sclereid nests, center (gray).—17. Sclerified axial phloem parenchyma cells.—18. Druses in secondary phloem ray (center strip two cells wide) and in adjacent phloem parenchyma cells (upper left, lower right).—19. Portion of sclereid nest with prominent rhomboidal crystals. Figure 16, magnification scale above Figure 1. Figures 17-19, magnification scale above Figure 4.

dict relationship (e.g., presence of vestured pits, presence of intraxylary phloem). Such features have distinctive systematic distributions but are not found in *Ticodendron*. The wood of Betulaceae differs moderately from that of *Ticodendron* in degree of phyletic advancement (data from Tipppo, 1938, and Metcalfe & Chalk, 1950). In Betulaceae, perforation plates are scalariform with numerous bars and axial parenchyma is diffuse as in *Ticodendron*. Somewhat more specialized in Betulaceae than the corresponding feature in *Ticodendron* is the presence of the fiber-tracheids (rather than tracheids). The rays of Betulaceae (Homogeneous Type I and III) are markedly more specialized than those of *Ticodendron* (Heterogeneous Type I), as is the alternate pitting of vessels (as compared to scalariform to opposite). Rhomboidal crystals are not present in wood of Betulaceae, but they are present in vegetative parts of the plant. Woods of Betulaceae may contain dark-staining deposits like those of *Ticodendron*.

Wood of Corylaceae (Betulaceae subfamily Coryleae of many authors) also shows resemblances to *Ticodendron*, but about the same degree of divergence in level of specialization (data from Tipppo, 1938, and Metcalfe & Chalk, 1950). In Corylaceae, perforation plates range from scalariform to simple and lateral wall pitting is alternate; fiber-tracheids are present; axial parenchyma is diffuse; rays are Homogeneous Type II, or have a small degree of heterogeneity (Heterogeneous Type IIB) in *Carpinus* and *Ostrya*. Wood of Corylaceae often contains dark-staining deposits like those of *Ticodendron*.

The occurrence of grouped vessels in Betulaceae and Corylaceae is not a specialized character independent of others. Vessels may be grouped in woody dicotyledons with fiber-tracheids or libriform fibers (degree of grouping depends on ecology), but vessels are solitary or nearly so in woods with tracheids (Carlquist, 1984), as in *Ticodendron*. Rhomboidal crystals, like those of *Ticodendron*, do occur in rays of Corylaceae.

There are no distinctive characters of systematic significance in woods of Betulaceae or Corylaceae that are not also found in *Ticodendron*. Fagaceae has many of the same features as Betulaceae and Corylaceae (e.g., crystals in ray cells), but wood is rather more specialized. Thus, comparisons to *Ticodendron* need not involve Fagaceae.

Bark anatomy, however, more clearly shows relationship between *Ticodendron* and the fagalean families (observations on these families original, based on material in the Rancho Santa Ana Botanic Garden wood slide collection). Fusiform nests of

sclereids, cells of which contain large rhomboidal sclereids, are found in bark of *Ticodendron*, *Corylus cornuta* Marsh. (= *C. rostrata* Ait.), *Betula pendula* Roth, and, in Fagaceae, *Lithocarpus densiflora* (H. & A.) Rehder. These highly distinctive sclereid nests alone might be evidence of relationship. In addition, druses in cortex, axial secondary phloem parenchyma, and phloem ray parenchyma characterize *Ticodendron*, *Betula pendula*, and *Corylus cornuta* (druses in cortex but rhomboidal crystals in axial phloem parenchyma occur in *Lithocarpus densiflora*). Subdivided phloem ray cells with a druse in each of the cells occur in *Ticodendron* and *Corylus cornuta*. *Ticodendron* does not have phloem fibers, but it has a possibly allied phenomenon, conversion of strands of axial phloem parenchyma to strands of sclereids. Phloem fibers do occur in *Betula pendula* and *Corylus cornuta*. Phloem fibers are absent in bark of some species of *Betula* and *Alnus*. *Ticodendron* has an external periderm, but evidently does not develop successive deep-seated periderms; deep-seated periderms are likewise absent in *Alnus*, *Betula*, and at least some Fagaceae.

Thus, there are no features in wood that rule out a relationship between *Ticodendron* and the families of Fagales (Betulaceae, Corylaceae, Fagaceae). The similarity in bark between *Ticodendron* and the families of Fagales offers positive evidence of relationship. Conceding a probable relationship between *Ticodendron* and Fagales, one must note the appreciably more primitive wood of *Ticodendron*. This accords with the rather primitive (compared to other Fagales) floral morphology of *Ticodendron* (Gómez-Laurito & Gómez P., 1989). *Ticodendron* can be considered a very primitive element in Fagales. It could not be included in any of the existing fagalean families without markedly altering the family description, with respect not only to wood anatomy but to other features as well (see other papers in this series). Therefore, wood and bark anatomy support placement of *Ticodendron* in a monogeneric family referred to Fagales. Wood and bark of other families considered earlier in discussions among the authors of other papers on *Ticodendron* were considered in comparisons: Brunelliaceae, Dilleniaceae, Juglandaceae, Myricaceae, Picrodendraceae, and *Nothofagus* (which several authors now segregate from Fagaceae). The anatomical resemblances between *Ticodendron* and these families are appreciably fewer than the resemblances between *Ticodendron* and Betulaceae and Corylaceae (or Coryleae of Betulaceae), and so such comparisons have been omitted.

LITERATURE CITED

- BAILEY, I. W. & W. W. TUPPER. 1918. Size variation in tracheary cells. I. A comparison between the secondary xylems of vascular cryptogams, gymnosperms, and angiosperms. *Proc. Amer. Acad. Arts* 54: 149-204.
- CARLQUIST, S. 1975. *Ecological Strategies of Xylem Evolution*. Univ. California Press, Berkeley.
- . 1984. Vessel grouping in dicotyledon woods: significance and relationship to imperforate tracheary elements. *Aliso* 10: 505-525.
- . 1988. *Comparative Wood Anatomy*. Springer-Verlag, Berlin & Heidelberg.
- FROST, F. H. 1930. Specialization in secondary xylem in dicotyledons. I. Origin of vessel. *Bot. Gaz. (Crawfordsville)* 89: 67-94.
- GÓMEZ-LAURITO, J. & L. D. GÓMEZ P. 1989. *Ticodendron*: a new tree from Central America. *Ann. Missouri Bot. Gard.* 76: 1148-1151.
- KRIBS, D. A. 1935. Salient lines of structural specialization in the wood rays of dicotyledons. *Bot. Gaz. (Crawfordsville)* 96: 547-557.
- . 1937. Salient lines of structural specialization in the wood rays of dicotyledons. *Bull. Torrey Bot. Club* 64: 177-186.
- METCALFE, C. R. & L. CHALK. 1950. *Anatomy of the Dicotyledons*. Clarendon Press, Oxford.
- TIPPO, O. 1938. The comparative anatomy of the secondary xylem of Moraceae and their presumed allies. *Bot. Gaz. (Crawfordsville)* 100: 1-99.